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Seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia spp.* in the southern Baltic Sea (Gdańsk Deep) – numerical simulations

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Abstract

A population dynamics model for copepods is presented describing a seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia spp.* in the southern Baltic Sea (Gdańsk Deep). The copepod model was coupled with an one-dimensional physical and biological upper layer model for nutrients (total inorganic nitrogen, phosphate), phytoplankton, microzooplankton and an early juvenile of herring as predator. In this model, mesozooplankton (herbivorous copepods) has been introduced as animals having definite patterns of growth in successive stages, reproduction and mortality. The populations are represented by 6 cohorts in different developmental stages, thus assuming, that recruitment of the next generation occurs after a fixed period of adult life. The copepod model links trophic processes and population dynamics, and simulates individual growth within cohorts and the changes in biomass between cohorts. The simulations of annual cycles of copepods contain one complete generation of *Pseudocalanus* and two generations of *Acartia* in the whole column water, and indicate the importance of growth of older stages of 6 cohorts each species to total population biomass. The peaks of copepods biomass, main, at the turn of June and July for *Pseudocalanus* and smaller, in July for *Acartia*, lag that phytoplankton by ca. two mouths due to growth of cohorts in successive stages and egg production by females. The numerical results show that the investigated species could not be the main factor limiting the spring phytoplankton bloom in the Gdańsk Deep, because the initial development was slow for *Acartia* and faster for *Pseudocalanus*, but main development formed after the bloom, in both cases. However, the simulated microzooplankton biomass was enough high to conclude, in our opinion, that, in this case, it was major cause limiting phytoplankton bloom. Model presented here is a next step in understanding how the population dynamics of a dominant species in the southern Baltic Sea interact with the environment.

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1 Introduction

In the past, where zooplankton has been introduced into a model, factors such as filtering, respiration, and excretion rather have often been taken as fixed productions of the hypothetical biomass rather than being related to more detailed information on behaviour and metabolism. In the literature there are now considerable experimental data on these aspects for several species of zooplankton. This information can be used to provide some idea of the functional relations which could be used in a simulation of zooplankton response to variations in its environment. The development of such theoretical descriptions is critical to the inclusion of these animals, as animals, in more general simulations of ecosystems. Most of models take into account only nutrient and phytoplankton (Fransz et al., 1991), probably because of the difficulty of representing the complex behaviour that exists among zooplankton species and also among the different zooplankton developmental stages. Models having one compartment for the whole zooplankton community are useful only for simulating ecosystem dynamics over the course of a few days (Wroblewski and Richman, 1987) or for a stable environment but become meaningless for long periods if the environment fluctuates. Although field workers consider population dynamics to be the minimum level of study zooplankton population models are rarely included in ecosystem models.

The considerations of herbivores as biomass show that useful deductions can be made. Especially in studies of phytoplankton populations, it may be sufficient to use a single parameter for grazing the general concepts from this point of view have already been reviewed (Riley, 1965). Such studies of phytoplankton usually stress the effects of physical variables in changing the phytoplankton populations. These factors are certainly important, but they may have been overemphasised by the excessive simplicity of the portrayal of the herbivores. Thus, it is necessary to look at the probable intricacies that can arise from more consistent consideration of growth, reproduction, and mortality of copepods on particular development stages. Steele and Henderson (1976) demonstrated that a comprehensive model of the food chain needs to take into

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account the population dynamics of herbivores for *Calanus finmarchicus* in the North Sea; this species dominates the biomass of zooplankton in spring and summer and shows clearly demarcated cohorts. The study of copepods population dynamics was made for instance by Francois Carlotti and several co-workers who have worked along the same lines, i.e. in the papers by Carlotti and Sciandra (1989), Carlotti and Nival (1992), Carlotti and Radach (1996), Carlotti and Wolf (1998) and Radach et al. (1998) and here should be included paper Moll and Stegert (2006). This type of study for the southern Baltic Sea (Gdańsk Gulf) has been made by Dzierzbicka-Głowacka (2005a) for *P. elongatus* dynamics in the spring bloom time in the Gdańsk Gulf. However, growth ad development of copepodite stages of *Pseudocalanus* were presented by Dzierzbicka-Głowacka (2004a, b).

The aim of this paper is description a seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia spp.* at the Gdańsk Deep. A population dynamics model for copepods was coupled with a 1-D physical and biological model (Dzierzbicka-Głowacka 2005b) and a simple of 1-D prey-predator upper layer model (Dzierzbicka-Głowacka 2006).

2 The coupled one-dimensional model

Recently, Dzierzbicka-Głowacka (2005b) developed a one-dimensional physical and biological upper-layer model. In our paper, we study a dynamics of *P. minutus elongatus* and *Acartia spp.* from the southern Baltic Sea (Gulf of Gdansk). We kept the strukture of both simple models (Fig. 1) and added a component for pelagic detritus, which was not previosly represented.

An one-dimensional Coupled Ecosystem Model consist of three submodels: meteorological, physical and biological: the meteorological component drives both 1-D models, and the output of the physical model is also used for driving the biological model. We do not discuss the meteorological and physical submodels, but focus on the biological submodel. This submodel combines two models: *nutrient-phytoplankton-*

zooplankton-detritus and *prey-predator*; i.e. this model consists of seven mass conservation equations. There are six diffusion advection reaction equations for phytoplankton, micro- and mesozooplankton, and early juvenille fish biomass and a double nutrient in the water column. The seventh equation, an ordinary differential equation, describes the development of detritus at the bottom. The equations, process formulations and parameter values of the ecosystem model are given by Dzierzbicka-Głowacka (2005b). However, the additional equations and processes relating to the model's pelagic detritus compartment are presented in Table 1.

The philosophy was to make the model as simple as possble as far as phytoplankton is concerned: phytoplankton is modelled with the aid of only one state variable. The phytoplankton concentration is taken as a dynamically passive physical quantity, i.e. it is incapable of making autonomous movements. The biological model incorporates formulations of the primary production mechanism and of the remineralization mechanisms within the mixed layer in the lower layers and at the bottom. Phytoplankton in the water is either grazed by zooplankton or else it dies and sinks. The grazed phytoplankton can be divided into many groups: one contributes to zooplankton growth, another is deposited as faecal pellets, and a third is excreted by the zooplankton as dissolved metabolites, and is losed by mortality and predation. Organic detritus in the water column is either immediately remineralized or directly transported to the bottom, where it accumulates in a stock of benthic detritus. The concept of the detritus pool at the bottom has been introduced to create a lag in remineralization of the majority of detritus and the eventual replenishment of the upper layer with nutrients. This complex process is parameterized by assuming a net remineralization rate for bottom detritus (Billen et al., 1991). In this model nutrients are represented by two components: total inorganic nitrogen (NO_3+NO_2+NH_4) and phosphate (PO_4). The pool of nutrients is enriched in many ways: through remineralization of dead phytoplankton, zooplankton and fish, and feacal pellets; release from phytoplankton; zooplankton and fish excretion and benthic regeneration. One state variable for microzooplankton is considered. Microzooplankton is defined as heterotrophic planktonic organisms from

10 to 500 μm SED (Spherical Equivalent Diameter) excluding heterotrophic nanoflagellates and naupliar/larval stages of larger zooplankton and of benthic organisms. The microzooplankton comprises ciliates and other heterotrophic protests, which are filter-feeders, feeding on phytoplankton. The fish is represented by earlier juvenile of herring *Clupea harengus* for 4–10 cm size class, where its growth rate is controlled by the encounter rate between consumer and prey. This component has been introduced into this model to determine a predation of zooplankton.

In this paper the mesozooplankton (herbivorous copepods) has been introduced into this model as animals having definite patterns of growth, reproduction, and mortality. Assume that two taxa of copepod *Pseudocalanus minutus elongatus* and *Acartia spp.* are present. The each species population is represented as six cohorts with different developmental stages.

3 Submodel of population dynamics for investigated copepods

We consider that the mesozooplankton is composed of 6 cohorts in different age of *P. m. elongatus* and *Acartia* spp. with weights W_i and numbers Z_i; then $\{Z_{\text{meso}}\} = \sum_{k=1}^{2} \sum_{i=1}^{6} W_i Z_i$, where

$$\frac{\partial W_i}{\partial t} = \text{ING}_i - \text{FEC}_i - \text{MET}_i \tag{1}$$

$$\frac{\partial Z_i}{\partial t} = \frac{\partial}{\partial z}\left(K_z \frac{\partial Z_i}{\partial z}\right) - \text{MIG}_i - \text{MOR}_i - \text{PRED}_i \tag{2}$$

Equation (1) determines the change in weight of an individual copepod taking developmental stages into consideration as the sum of its individual gains and losses of energy (GROWTH=ING-FEC-MET); Eq. (2) represents the effects of mortality, predation, and daily migration on a particular cohort as a function of numbers in that cohort in appropriate development stage. If W_{egg} the weight of the naupliar stage at which

feeding starts and W_{female} is the weight of the adult, the for each cohort relations of the form Egg=$F(T, \text{Foot}, Z_{female}, W_{female}/W_{egg})$ indicate the requirements for some function defining recruitment Egg in terms as temperature, food available, Foot, adults numbers, Z_{female}, and the ratio of adult to naupliar weight, W_{female}/W_{egg}.

Processes taken into account are presented in Table 2. Weight is controlled by growth, which depends on food and temperature. The growth rate is expressed in carbon mass units. The ingestion rate ING for specific developmental stages is dependent firstly on the food concentration according to a function fil_i a secondly on temperature, following a constant Q_{10} law fte_i. We use the allometric relation expressed by Paffenhöfer (1971), fw_i, in which the maximal ingestion rate increases with weight during development. Egested matter is the part of ingested matter which is not assimilated and here is represented by fecal pellet production FEC. The quantity of egested matter is simply proportional to the ingestion rate with percentage of ingestion egested as fecal material n_f. The total rate of metabolic loss (excretion rate) MET can be split into three components with different relations to the food uptake rate (see Steele and Mullin, 1977). M_s is assumed to be the resultant or basic metabolism, independent of food supply. The respiratory costs of foraging for and capturing food M_r should fall as the food concentration and, correspondingly, f(Foot), rises. Finally, there is the cost of assimilating and biochemically transforming the food (specific dynamic action, M_a), proportional to the rate of assimilation A which is computed as a constant fraction of the ingestion rate (e.g. Steele, 1974, who used A=0.7ING). We suppose as Wroblewski (1984) that excretion can be separated into 2 terms. The first (M_s) represents the basic metabolism and is proportional to weight. The second (M_a) refers to the active metabolism and is proportional to ingestion rate.

The number of juveniles EGG is defined assuming that eggs are released by the female throughout some time span J. For mature adults, ingested matter is used for maintenance and reproduction (Sekiguchi et al., 1980). The reproductive rate per individual female of *Pseudocalanus* can be converted to the equivalent amount off egg matter per day as a percentage of female weight (see Corkett and McLaren, 1978,

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McLaren and Leonard, 1995). The efficiency term X is the conversion of increase in biomass by the adult population into eggs, including the wasted growth in the males.

The intensity of mortality MOR is determined as average mortality rate m_z. m_z at different food concentrations and temperatures for *Pseudocalanus* is given by Klein Breteler et al. (1995).

According to Mudrak (2004), the youngest development stages (nauplii) were usually found in subsurface layers (mostly between 10 and 20 m). They did not normally change their positions in the water column. Younger copepodids (C1–C2) showed strong diel vertical migration above the halocline, older copepodids (C4–C5) below the thermocline, when adults remained in the deepest part of the water column (near the bottom) (Mudrak et al., 2004). Therefore, here the migration process MIG only for copepodids in the vegetation season was described in a day-night cycle where $f(z)$ is the vertical distribution of copepods in time t_o in which the its maximum concentration occurs in the upper layer.

Predation PRED represents the losses incurred by Z_i. Its magnitude can be determined from the biomass of early juvenile herring on the assumption that the loss incurred by the prey concentration is proportional to the increase in the predator biomass.

4 Adaptation of the submodel to investigated copepods

Planktonic copepods are the major food source for fish larvae in the period of development following the utilization of the larval yolk sac. They also form part of the basic diet of many adult pelagic fish. Feeding studies of fish larvae by Załachowski et al. (1975) and Last (1978a, b, 1980) have shown that *Pseudocalanus*, *Acartia* and *Temora* nauplius and copepodid stages are important components of the diet of numerous species of fish in the Baltic Sea and adjacent waters; i.e. the North Sea and also the English Channel as well as in Scotland, Nova Scotia and Canadian Arctic waters.

Copepod ingestion and egg-production rates vary in response to forcing from the physical and biological environments (Runge, 1984, 1985; Ambler, 1985; Peterson,

1988; Rothschild, 1988; Kleppel, 1992). In turn, ingestion rate and diet are thought to affect growth, development and egg production (Roman, 1984; Stoecker and Egloff, 1987; Kleppel et al., 1991). The relationships between food concentration, composition, feeding and production have been difficult to quantify in natural food environments. Growth and development of copepods in different waters are determined mainly by temperature and food availability (Paffenhöfer and Harris, 1976; Corkett and McLaren, 1978; Vidal, 1980a, b; Thompson, 1982; McLaren et al., 1989; Klein Breteler et al., 1995; Witek, 1995; Koski et al., 1998; Dzierzbicka-Głowacka, 2004a, b). Egg production of copepods in nature is generally assumed to be food-limited, while juvenile growth often seems to be dependent on temperature alone (McLaren et al., 1969; Paffenhöfer and Harris, 1976; Thompson, 1976; Corkett and McLaren, 1978; Landry, 1983; Dzierzbicka-Głowacka and Zieliński, 2004). Some authors found correlations between copepod egg production and phytoplankton standing stock (e.g. Landry, 1978; Checkley, 1980; Durbin et al., 1983; Beckman and Petersen, 1986; Kiørboe and Johanson, 1986), while others did not e.g. (Bautista et al., 1994; Hay, 1995).

Most of the coefficients used in the submodel are calculated from these results. Where data are lacking, coefficients are estimated from knowledge about similar species. The parameters of the function fil – the dependence of the ingestion rate on the food concentration – are ($f_{i_{\max}}$) the maximal ingestion rate, (Foot$_o$) the minimal threshold food concentration is the value of Foot at which GROWTH=0, and (k_{Foot}) the ingestion rate as $f_{i_{\max}}/k_{\text{Foot}}$ for Foot is slightly greater than Foot$_o$ (Steele and Mullin, 1977).

The ingestion rate depends on the developmental stage, food supply, temperature and weight of the animals. We assumed that the first two naupliar stages of *Pseudocalanus* and *Acartia* are unable to ingest particles; they are considered to live on reserves provided by the egg after Berggreen et al. (1988) for *Acartia tonsa*. For the other naupliar stages, N3–N6, we have extrapolated the coefficient $f_{i_{\max}}$ considering a similar increase as for C1. The values of $f_{i_{\max}}$ for C1 – adults were estimated after experimental data which were given by Ciszewski and Witek (1977) for *P. m. elongatus*

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at 5°C and *Acartia bifilosa* at 15°C from the Gdańsk Depth. The parameters ($Foot_o$) and (k_{Foot}) for copepodite stages of *Pseudocalanus* were computed by Dzierzbicka-Glowacka (2003, 2004a, b) after Vidal's data as quantitave expressions in the 8–15.5°C temperature range. For temperature below 8°C, $Foot_o$ and k_{Foot} were assumed like for T=8°C, and for temperature above 15.5°C, like for T=15.5°C. However, for nauplii and adults, the values were assumed as for C1 and C5, respectively.

Wlodarczyk et al. (1992) determined a threshold food concentration for adult females of *Acartia hudsonica* which fed *Thalassiosira constricta*. There thresholds corresponded to carbon concentrations of 30.5, 11.6, 20.7 and 16.4 mgC m^{-3}, and were not significantly different at the 4 temperatures: 4, 8, 12 and 16°C. These values were similar to given by Durbin and Durbin (1992) who used the same clone of *T. constricta* but of a larger mean cell size. Value of $Foot_o$ was comparatively high in *A. tonsa* fed the small alga *R. baltica* (45 mgC m^{-3} – Kiørboe et al., 1985) and low for large species like the dinoflagellate *G. fissum* (0.2–22 mgC m^{-3} – Piontkovski and Petipa, 1976). Turner and Tester (1989) made extensive measurements of feeding by *A. tonsa* females upon natural assemblages dominated by diatoms and dinoflagellates. Their figures suggest thresholds at 5 to 10 mgC m^{-3}. We chose a $Foot_o$ of 20 mgC m^{-3} for larger copepodite C3–C5 and adult stages, but a lower threshold of 10 mgC m^{-3} for nauplii and smaller copepodites.

Ingestion and egg production by adult *Acartia hudsinica* (at 5°C) and *Acartia tonsa* (at 10°C) was measured in the laboratory by Verity and Smayda (1989). Although these investigators did not analyze their data for the existence of k_{Foot} at 60 to 75 mgC m^{-3}. We assume that the k_{Foot} is equal to 70 mgC m^{-3} for copepodite and adult stages, but for nauplii 28 mgC m^{-3} like a mean value of k_{Foot} for C1 of *Pseudocalanus*.

The maximum ingestion rate in copepods has been shown to be temperature dependent, but the reported Q_{10} values differ widely (3.8 for *Centropages hamatus* – Kiørboe et al. (1982); 5.4 for *Neonalanus plumchrus* – Dagg and Wyman (1983); 4.1 for *Eudiaptomus graciliodes* – Christofferson and Jespersen (1986); 2.4 for *Temora longicormis*, and 2.2 for pooled data from several species – Dam and Peterson (1988); 1.88 for

Acartia hudsonica – Wlodarczyk et al. (1992). The maximal ingestion rate increase exponentially with temperature following a Q_{10} varying from 1.4 to 3.9 for *Acartia tonsa* – Thompson et al. (1994); from 1.6 to 3.3 for *Acartia clause* – Kremer and Nixon (1978)). We use an intermediate value of 2.6 for *Acartia* to estimate the t_2 coefficient; consequently our parameter t_2 has a value of 1.1. However, for *Pseudocalanus* a Q_{10} of 1.9 was assumed after Fennel (2001); hence a t_2 has a value of 1.066. Coefficient t_1 is calculated so that fte is equal to 1 at 15°C for *Acartia* and 1 at 5°C for *Pseudocalanus* and therefore t_1 is equal to 0.239 and 0.726 for *Acartia* and *Pseudocalanus*, respectively. Coefficients Foot_o, t_1 and t_2 are identical for all stages. The exponent α of the allometric relation between weight and ingestion generally lies between 0.6 and 0.8 for copepods (Paffenhöfer, 1971). We adopt a value of 0.7 for all the stages. The assimilation rate (n_a) of 70% is generally considered as representative for copepods (Steele, 1974); hence the percentage of ingestion egested as fecal material (n_f) is 30%. Supposing first that 30% (n_e) of the ingested matter is used for metabolism and is excreted, and second, that the ratio of maximum ingestion rate to weight averages 20% (Sciandra, 1986), a daily excretion rate of 6% of weight may be attributed to the active metabolism. To adjust total metabolic losses to an average value of 10% of weight per day (Corkett and McLaren, 1978; Miller and Landry, 1984), We estimate that excretory wastes due to minimal metabolism (n_w) represent 4% of the body weight (Carlotti and Sciandra, 1989). The growth rate for copepodite stages of *Pseudocananus* at 5°C and *Acartia* at 15° is shown at Fig. (2) as a function of food concentration.

Quantitative expressions describing the effects of temperature and cephalothorax length on the rate of production of egg matter ProdEgg for some geographically separete populations of *Pseudocalanus spp.* except *Pseudocalanus* from the Baltic Sea were presented in Dzierzbicka-Głowacka and Zieliński (2004).

The hypothesis that food-saturated rate of production of egg matter is equivalent to maximal specific growth rate of copepods was tested. Studies were made by some (Sekiguchi et al., 1980 for *Acartia clasi*; Berggreen et al., 1988 for *Acartia tonsa*; Fryd et al., 1991 for two species of *Centropages*; McLaren and Leonard, 1995 for four species

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of *Calanus* and Dzierzbicka-Głowacka, 2005c for *Pseudocalanus*). Here we consider above hypothesis for obtained the numbers of eggs produced per female per day as a function of growth rate, i.e. multiplying exp GROWTH-1 by W_{female}/W_{egg} assuming maximum growth rate of *Pseudocalanus* for C5 and of *Acartia* for C1. The number of juveniles is defined on the assumtion that eggs are released by the adult female throughtout some time span J. Corkett and McLaren (1978) have suggested that the mean reproductive span for *Pseudocalanus* was 51 days, and their average life time between the appearance of the last sac and death was 41 days, i.e. the average longevity of females was 92 days. The period of egg production was also determined by Thompson (1982) for *Pseudocalanus elongatus* from the North Sea and was 39 days. He suggested that the post-reproductive period may last as long as the reproductive period. However, for females from the southern Baltic Sea this value for *Acartia bifilosa* changed with temperature from 20°C to 7°C – from 2 weeks up to about 30 days; for *Pseudocalanus minutus elongatus* – species living in cooler waters than *Acartia* – was about 40 days in temperature of 7°C and after about 2 months in temperature of 3°C after Ciszewski and Witek (1977). We assume a sex ratio (X) of 80% for females of *Pseudocalanus* and 20% for females of *Acartia* after experimental data for 1999 in May in the Gdańsk Depth (Mudrak 2004). In this study the weight of an egg W_{egg} is assumed as 0.14 μgC egg^{-1} for *Pseudocalanus* (Frost, 1989) and 0.0305 μgC egg^{-1} for *Acartia* (Ambler, 1985). The wet weight adult of females is obtained after standard HELCOM (Hernroth, 1985) assuming organic carbon content of copepods gC/g$_{w.w.}$=0.064 (Vinogradov and Shushkina, 1987).

Schmidt et al. (1998) found the mortality of *Acartia tonsa* in the southern Baltic Sea, ca. 7% in winter, 5% in autumn, and negligible in summer and spring (ca. 1%). We use above value for *Acartia*. However, for *Pseudocalanus* the mortality rate (m_z), as a function of temperature and food concentration, is used after Klein Breteler et al. (1995). The average mortality rate of *Pseudocalanus* is shown at Fig. (3) in the upper (euphotic) layer and lower one.

The parameters of migration MIG are the relative amplitude of zooplankton concen-

tration changes (a_w) and the time in which the maximum zooplankton concentration occurs (t_o). The values of 0.6 and 3.25 a.m. for a_w and t_o were estimated by Renk et al. (1983) on the basis of experimental data for the southern Baltic Sea. The vertical distribution of zooplankton in time t_o in the vegetation season was determined as a function of depth ($f(z)=-0.0003775z^2+0.62$) (Dzierzbicka-Głowacka, 1994). Figure (4) shows the diel migration as a function of depth at the four time: 03:00 a. m., 08:00 a. m., 03:00 p. m. and 08:00 p. m.

We use a value 5/3 for β in predation PRED, this means that 60% of ingested food is contributed to predator growth and 40% is voided as fecal pellets and excreted material. The detailed description of the process is presented in the work of Dzierzbicka-Głowacka (2005b).

5 Assumptions of the model

The dynamical constants used in the biological model with population dynamics submodel for copepods investigated were determined mostly from data derived from the literature (see Tables 1 and 2 of Dzierzbicka-Głowacka, 2005b). A in choosing values of parameters reasonably close to levels found in Baltic waters.

We need to make assumptions concerning the vertical distribution of biological characteristics and biology of the *Pseudocalanus* and *Acartia*: (i) initial values of the biomass of phytoplankton (Phyt=0.01 mgC m^{-3}) and microzooplankton (Z_{micro}=0.1 mgC m^{-3}) biomass and the total inorganic nitrogen (Nutr$_N$=6 mmol m^{-3}) and phosphate (Nutr$_P$=0.6 mmol m^{-3}) concentrations as constants with depth were assumed; (ii) assumed that the initial biomass of predator (3 cohorts) was B_1=30 mgC m^{-3} for concentration 4 ind. m^{-3} of 1st cohort at the end of June, plus B_2=15 mgC m^{-3} of 2nd cohort at the end of July and B_3=7.5 mgC m^{-3} of the 3rd cohort at the end of August. (iii) the mean weight for specific development stages of species investigated were assumed after standard HELCOM (Hernroth 1985) for Gdansk Deep; (iv) the initial population of *Pseudocalanus* had no eggs and no nauplii N1–N6, 2300

C1, 1800 C2, 1300 C3, 900 C4, 500 C5, and 300 adults m^{-2}, for a total biomass ca. 4.2 mgC m^{-2} in the whole column water; (v) the initial population of *Acartia* had no eggs and no nauplii N1-N6, 1100 C1, 1000 C2, 900 C3, 700 C4, 450 C5, and 300 adults m^{-2}, for a total biomass ca. 2 mgC m^{-2} in the whole column water.

We assume that the available food concentration for all the stages of the population of copepods investigated is the value of food concentration (phytoplankton and other resources) as well as copepods feed continuously if there is food present. The products of mesozooplankton metabolism, which enter the nutrient model (i.e. excretion, remineralized fecal pellets and dead bodies), are evenly distributed throughout the upper layer (Table 3). The remaining fecal pellets and dead bodies fall immediately to the benthic detritus.

Predator is represented by early juvenile of herring *Clupea harengus* (4–10 cm). The Vistula Lagoon is an important spawning area for southern Baltic spring-spawning herring *Clupea harengus*. At the turn of winter and spring (in March) , adults migrate from the southern Baltic to the spawning are in the shallow and brackish water of the Vistula Lagoon (Fey, 2001). Herring in the Vistula Lagoon has three cohorts each year (Margoński, 2000). Larvae abundance in Vistula Lagoon in 1999 was observed 495–128 individuals in 100 m^3. When young herring are about 40 to 50 mm, they undergo metamorphosis, developing the morphological characteristics of adults; they are then identified as juveniles. Metamorphosis begins in June in Vistula Lagoon. Herring early juveniles emigrated from the Polish part of the Vistula Lagoon; the juveniles of the first cohort migrated in June, the second cohort in July, and the third cohort in August to the southern Baltic Sea. An early juvenile (ca. 40 mm) appears in the Gulf Gdańsk after two weeks assuming that its velocity was ca. 4 cm s^{-1} after Miller et al. (1988). Therefore, in this calculations was assumed that, during the first half of year, the predator biomass B=0.

6 Results

The 1-D biological upper layer model detail described in Dzierzbicka-Głowacka (2005b), with the population dynamics submodel for copepods was used in the numerical simulations of the seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia* spp. in the southern Baltic Sea.

The flow field and water temperature used as the inputs of the biological submodel were reproduced by the physical submodel. However, wind stress, global radiation and the heat balance at the sea surface are determined from standard meteorological components for point (54°52′ N, 19°10′ E) in Gdańsk Gulf for 1999. In paper Dzierzbicka-Głowacka (2005a) I simulated the spring phytoplankton and *Pseudocalanus elongatus* dynamic in the southern Baltic Sea at the two stations. Here we present results of the biological parts of the model for 1999 at the Gdańsk Deep as well as we present the simulation made with a dynamic population of *Pseudocalanus elongatus* and *Acartia* spp.

6.1 Simulations of annual plankton cycle

Modeled temperature fields resulting from the physical model (as the output) (Fig. 5a) were used for the primary production, phytoplankton respiration and physiological processes of copepods calculation. The simulated temperature began to increase the second half of March and reached ca. 21°C in August. The destruction of the thermocline starts in the late fall. Probably, the spring bloom in this year was triggered in the first half of March. The bloom is initiated by the heating event and the extremely low winds. The end of permanent overturning of the water column in mid-March in the main event which allows the phytoplankton to start growing (Fig. 5b). The depths of the upper layer, which are determined by the mixing intensity in the water column, show that strong gradients in the nutrient concentration develop (Fig. 5c and d). The phytoplankton biomass (Fig. 5e) reflects the nutrient availability, showing a strong nutrient – depleting spring bloom. The phytoplankton biomass reached the mean maximum

values ca. 400 mgC m^{-3} in the upper 10 m layer in the spring bloom. The highest value occurred in the second half of April and equaled ca. 530 mgC m^{-3} on the surface sea (Fig. 5e). This situation is caused by the high nutrient concentrations and daily global radiation in the last decade of March and April. The phytoplankton biomass was low in summer from June till August most likely as a result of faster depletion of nutrients and the phytoplankton grazing by micro- and mesozooplankton. The development of microzooplankton was exactly correlated with the development of phytoplankton (Fig. 5f). Generally the greatest amounts of microzooplankton occurred in the upper layer, in the periods of large biomass of algae. Biomass of microzooplankton was characterized by the occurrence of two biomass peaks in a year; at the turn of summer and autumn. Considerable increase in Z_{micro} took place in April, shortly after the beginning of the spring bloom. The microzooplankton biomass was ca. 30 mgC m^{-3} in the spring time; however in the summer time, it fell below 10 mgC m^{-3} with simultaneous decreasing phytoplankton biomass and reappeared in early autumn with higher biomass. Small pelagic detritus (Fig. 5g) was abundant mainly when the phytoplankton concentration exceeded 200 mgC m^{-3}, and its maximum concentration was deeper than the 20 m layer.

The biomass of mesozooplankton, represent by *Pseudocalanus* and *Acartia*, increased in the first half of year reaching maximum values from ca. 8 mgC m^{-3} at the turn of June and July (Fig. 5h). This increase was mainly by growth in successive stages, mortality and egg production. In autumn a certain increase in phytoplankton biomass took place. *Phyt* remained stable, at a level slightly higher than in summer. It might have been related to the considerable reduction in the amount of micro and mesozooplankton, as well as an increase in concentration of nutrient resulting from deeper mixing of water. The vegetation season ended in December, when the biomass of phytoplankton dropped to a level from January–February. The early juvenile of herring biomass increased to ca. 60 mgC m^{-3} at the end of July, and 90 mgC m^{-3} at the end of August (Fig. 5i). The increase in predator biomass in July and August is additionally caused by migration of second and third cohorts from the Vistula Lagoon. The

highest biomass of early juvenile of herring occurred in last summer (ca. 140 mgC m^{-3}), when prey concentration reached the second, small, maximum.

6.2 Simulations of annual investigated copepods cycles

The copepod population model simultaneously provides the time variations for weighs and number of six cohorts and for biomasses of each cohorts for *Pseudocalanus minutus elongatus* and *Acartia spp.* in the whole column water in the southern Baltic Sea.

6.2.1 *Pseudocalanus minutus elongatus*

The distributions shown in Fig. 6 present the changes in values of weights W_i (Fig. 6a) and numbers Z_i (Fig. 6b) and biomasses of six cohorts $W_i Z_i$ (Fig. 6c) of *Pseudocalanus*.

One complete distinct generation (6th cohort of 2nd generation) developed throughout the seven mouths, beginning in mid-April and ending in mid-November.

The peaks of biomass (see Fig. 6c) were due to egg production, in mid-April – of 6th cohort of the 1st generation, at the turn of May and June – of 5th cohort as well as to a high degree of 6th cohort biomass, in mid-June – of 4th cohort as well as to a high degree of 6th cohort biomass and to a lower degree of 5th, at the turn June and July – of 3rd cohort as well as to a high degree of 6th cohort biomass and to a lower degree of 4th and 5th, in mid-July – of 2nd cohort as well as to a high degree of 6th cohort biomass and to a lower degree of 3rd, 4th and 5th cohorts biomass and at the first half of August – of 1st cohort as well as 2nd, 3rd, 4th, 5th and 6th cohorts biomass of the 1st generation.

The phytoplankton peak in September permitted a new growth period for the second generation copepodite stages (visible mainly in the weight curves); and females of 6th cohort produced a relatively small number of eggs to given a third generation in November.

The total depth integrated biomass of *Pseudocalanus* is characterized by one peak

biomass. The maximum total biomass (ca. 330 mgC m^{-2}) was at the turn of June and July (see Fig. 6c). Fig. 6 clearly illustrates the overlap between the first and second generations. The second generation, present the first spawning, seemed to develop slowly and a higher mortality.

During winter, the total biomass of *Pseudocalanus* slightly decrease, invisible at Fig. (6c), because of a weights decrease of individuals subject to lack of food (see Fig. 6a) as well as of a numbers decrease to enough low of mortality. The biomass then increased as results of considerable increase of individuals weight for the copepodite stages. In spring, the individuals became active and they grew by feeding on the phytoplankton bloom, and the adult females produced eggs. By combining the information on growth with the dynamics of individuals, we can affirm that most individuals had a lower growth rate during the naupliar and copepodite phases with a low phytoplankton biomass in summer; subsequently, the copepodite stages resumed exponential growth with the rise of phytoplankton in September (Fig. 6a). Individuals of 3rd generation were produced in November by the females of 6th cohort of 2nd generation, but they developed no farther than stage N3 because of the lack of food and the severe decrease in temperature. Growth curves stopped because of the death of individuals and which weights and numbers decrease. Any decrease in numbers was caused by mortality and at the second half of year, also by predation. The rate of mortality was high in summer in upper layer as result of high temperature and low food concentration; however, in spring time, one was the lowest as result of high food concentration and low temperature. Predation was the largest in October, when the predator biomass had maximum value.

6.2.2 *Acartia spp.*

The distributions shown in Fig. 7 present the changes in values of weights W_i (Fig. 7a) and numbers Z_i (Fig. 7b) and the depth integrated biomasses of six cohorts and total biomass $\sum_{i=1}^{6} W_i Z_i$ (Fig. 7c) of *Acartia spp.*

Two complete, from eggs to adults, distinct generations, for the first times – 6 cohorts of 2nd generation, the second times – 5 cohorts of 3rd generation, developed throughout the year, one beginning in April and the other from mid-June to mid-July (see Figs. 7a and b). The total biomass of *Acartia* is characterized by two biomass peaks, in July - main, and small, in September. The peak of biomass in July (ca. 140 mgC m^{-2}, see Fig. 7c) was mainly due to the high egg production by adults of the 2nd generation (1st, 2n, 3rd and 4th cohorts) as results of the very high numbers of adults (Fig. 7b). Figs. 7a and b clearly illustrates the overlap between generations. The 3rd generation, present from the first spawning in mid-June by 6th cohort to the adults at the turn of August and September as well as the first spawning at the turn June and July by 5th, 4th, 3rd, and 2nd cohorts to the adults in September, seemed to developed slowly (Fig. 7a) and had a high predation rate (Fig. 7b); i.e. the total development time of 6th cohort was 75 days and of 2nd cohort – 90 days. The second peak of biomass in September (ca. 70 mgC m^{-2}, see Fig. 7c) was mainly due to the high egg production of adults of the 6th cohort of 3rd generation (Fig. 7b) as result of high temperature. The phytoplankton peak in September permitted a new growth period for the 3rd generation copepodite stages, and females of 5th, 4th, 3rd, and 2nd cohorts of 3rd generation produced a relatively small eggs to give a 4th generation in October.

In the spring bloom, a substantial growth of phytoplankton biomass was observed which fell at the next stage as a result of an increase first of microzooplankton, and next mesozooplankton biomass. This growth in biomass of successive cohorts of copepods is caused by an increase of body weight and egg production by each of the adult. This situation leads to the substantial growth in the total biomass, $\sum_{k=1}^{2} \sum_{i=1}^{6} W_i Z_i$, which is the algebraic sum of products of weights, W_i, and numbers, Z_i a both species.

The biomass peak of *Pseudocalanus* appeared at the turn June and July; however, *Acartia* biomass was characterized by two biomass peaks in a year; in July and in September.

These small maxima occurring in the distributions of investigated species are the results mainly of a brood by successive cohorts causing their numbers to increase. The

calculations demonstrate that the growth of weight of each cohort is mainly caused by temperature and a substantial increase of phytoplankton biomass. The body weight of copepods strongly increase in the spring bloom because in the time the growth rate is higher as result of larger phytoplankton biomass. In this period, temperature has also significant influence on growth of *Pseudocalanus* causing the growth rate tends to maximum.

7 Discussion

The simulated biological characteristics (i.e. the inorganic nitrogen and phosphate concentrations, the phytoplankton biomass and depth integrated of *Pseudocalanus minutus elongatus* and *Acartia spp.* biomass) in the model were compared to the observations from the investigated water regions. Taking into consideration the fact that outputs of the meteorological submodel were obtained using meteorological data for 1999, the comparison of numerical results will made to the mean values of empirical data for 1999 on the based various authorities.

The outstanding problem concerns the quality of field data used to test such simulations. The problems of data arise from the fact that the variability in space and time of zooplankton is usually so great that any model that has the right orders of magnitude in its outputs will fit the data. Thus even with models treating herbivores in some detail, the testing of these models may rest primarily upon the nutrient and phytoplankton levels, which can be measured with greater accuracy.

The differences between the simulated and mean observed values of nutrient in the upper layer (0–15 m) were in the 0.5–1 mmol m^{-3} range for total inorganic nitrogen and ca. 0.1 mmol m^{-3} for phosphate (see Fig. 8). The higher errors (ca. 30%) were in the near-bottom layer (see Figs. 5c and d).

Phytoplankton biomass is more often measured as chlorophyll-a than as carbon. Samples of chlorophyll-*a* concentration were collected in two determined layers: 0–10 m and 10–20 m (see Maritime Branch Materials, IMGW 2000). Fig. 9 shows, the

first maximum of chlorophyll-*a* concentration noted in the upper 10 m layer in March (ca. 3.5 mg m^{-3}) and in April (ca. 2 mg m^{-3}) in both layers; however, the second maximum observed in August (ca. 2.5 mg m^{-3}). The values of surface chlorophyll-*a* were also obtained by Kaczmarek (unpublished data, Regional Oceanographic Database of Polish Institute of Oceanology) (see Fig. 9). From the second half of March to the end of April, in the spring bloom time, chlorophyll-*a* ranged from nearly 3 to about 25 mg m^{-3} in the 30 m layer in the Gdańsk Deep. The mean concentration of chlorophyll-*a* was ca. 4.5 mg m^{-3} in the upper 20 m layer on 21 March and on 25 April, ca. 7 mg m^{-3} in the upper 10 m and 5 mg m^{-3} in the 10–30 m layer; however, the very high concentration (ca. 25 mg m^{-3}) was found in the morning on 25 April on the surface (in the 2 m layer). To compare the simulated results forphytoplankton carbon to available chlorophyll-*a* data, a C/Chl-a ratio has to be assumed for converting the simulated carbon contents to chlorophyll-a. Literature mean value for the C/Chl_a ratio lies between 31 for open water of the southern Baltic Sea and 43 for coast water in the upper layer (see Table 1 of Renk, 2000). However, Witek (1993) given the ratio of carbon amount in phytoplankton to the amount of chlorophyll-*a* in the Gdańsk Gulf (Fig. 4.2.4. of Witek 1993) and it, in the spring season in the surface layer, was 2–4 times greater than in the remaining part of the year. This means that in the spring season smaller amounts of chlorophyll-*a* in the cell were sufficient for the growth of algae. Thus, in the upper layer (10–30 m), the mean observed values of the chlorophyll-*a* content of ca. 5 mg m^{-3} corresponds to 155 to 215 mgC m^{-3} after Renk (2000) and to 110 to 275 mgC m^{-3} in March and April, respectively, after Witek (1993). However, in the surface 10 m layer in April, the mean chlorophyll-*a* content of ca. 10 mg m^{-3} corresponds to 310 to 430 mgC m^{-3} after Renk (2000) and to 550 mgC m^{-3} after Witek (1993). The chlorophyll data and the simulated phytoplankton biomass are enough well correlated and attain their maximum concentrations in April, which are of similar magnitude, depending on the conversion factor C/Chl_a. In this paper, the calculations were made assuming the C/Chl-a ratio as mean value for the southern Baltic Sea in the upper layer after (Witek, 1993), because using this ratio, the obtained values are the most similar to the observed ones.

The most important species in the Gdansk Gulf are *Acartia* spp. (i.e. *A. bifilosa*, *A. longiremis* and *A. tonsa*) and *Centropages hamatus*, *Temora longicornis*, and *Pseudocalanus minutus elongatus*. In the Gdańsk Deep a fourth species *Pseudocalanus* occurred in great abundance, which in deeper layer, below 30 m, became the dominant, and below the isohaline layer - almost the only representative of mesozooplankton. In 1999 at the Gdańsk Deep, predominant species were *Pseudocalanus elongatus* and *Acartia longiremis* (see Maritime Branch Materials, IMGW 2000). The results of the numerical simulations described here are compared to the mean observed values assuming organic carbon content of copepods $gC/g_{w.w}$=0.064 (Vinogradov and Shushkina, 1987). The mean biomass of all copepods (8 species), in the whole column water in the Gdańsk Deep in 1999, was obtained by (see Maritime Branch Materials, IMGW 2000), i.e. in March – ca. 20, April – ca. 45, June – ca. 80 and August – ca. 100 $mg_{w.w}\,m^{-3}$ and it corresponds to 1.3, 2.9, 5.1 and 6.4 $mgC\,m^{-3}$. However, the mean biomass of investigated species calculated here was ca. twice lower than observed values except March; i.e. in March – ca. 0.1, April – ca. 1.2, June – ca. 2.8 and August – ca. 3.8 $mgC\,m^{-3}$.

The plankton material also was collected in 20–25 May 1999 in diurnal cycles from the water column, which was divided into several layers. The hauls were made using a Copenhagen net (100 μm). Every single sample was prepared and analysed according to standard methods (HELCOM). Numbers of *P. m. elongatus* and *Acartia spp.* for specific development stages were given by Mudrak (2004). During this period, the vertical distributions of observed biomass in diurnal cycles were different, i.e. in the 0.07–0.8 $mgC\,m^{-3}$ range in the upper-euphotic layer and 0.1–0.9 $mgC\,m^{-3}$ in the lower one for *Pseudocalanus* and 0.02–1 $mgC\,m^{-3}$ in the upper layer and 0.03–0.55 $mgC\,m^{-3}$ in the lower one for *Acartia*. The average value of biomass in the whole column water in these days was 0.395 $mgC\,m^{-3}$ for *Acartia* and 0.728 $mgC\,m^{-3}$ for *Pseudocalanus*.

Figures 6–7 show the results of numerical simulations and observed data for depth integrated biomass of investigated species. Depth integrated biomass was in the 1.8–42 $mgC\ m^{-2}$ range for *Acartia* and in the 6–63 $mgC\,m^{-2}$ range for *Pseudocalanus* at

the end of May after experimental data. However, the observed mean values were 13 mgC m^{-2} for *Acartia* and 48 mgC m^{-2} for *Pseudocalanus* and they are slightly higher (ca. 25%) for *Acartia* and ca. 20% lower for *Pseudocalanus* than ones-mean obtained here, i.e. the calculated mean biomass was ca. 10 mgC m^{-2} for *Acartia* and ca. 60 mgC m^{-2} for *Pseudocalanus*.

The results obtained here, are differ than these given by Mudrak (2004) and Maritime Branch Materials (2000), probably for predation, which is proportional to the increase in predator biomass. During the first half of year, predation was assumed zero because predator biomass was equal to zero in this time; however, during the second half of year predation was considered, because, in our model, predator is only represented by early juvenile herring. High biomass of *Pseudocalanus* in May was due to too large initial numbers of adults which produced too many of eggs in April (too hight the efficiency term X) and too low biomass of *Acartia* in May was due to too small initial numbers of adults which produced too little of eggs in April (too low the efficiency term X), and too a low mortality for *Pseudocalanus* and a high for *Acartia* in numbers in the spring time as well as the low threshold for ingestion of food causing an early increase in weights. This situation could be also cause by migration which, in our model, is of the same for copepodites of investigated species.

In our model, the development of copepods adjusts to the dynamics of its food supply. The threshold of food concentration which copepods can survive seems to be an essential parameter at the beginning of the bloom and at the end of summer. Copepod biomass depends on physical and biological processes, such as phytoplankton growth as well as mortality and predation. We established a low threshold for naupliar and copepodite stages. The simulations show that the zooplankton population clearly misses the phytoplankton bloom if it is brief. One complete generation of *Pseudocalanus* develops in spring, summer and early autumn. Any increase in *Pseudocalanus* population starts in spring bloom time (Fig. 6c) but mainly formed at the turn of spring and summer from individuals of the second generation. Two complete generations of *Acartia* develop in spring and summer. In the case *Acartia*, the initial growth in popu-

lation takes place in May after the phytoplankton spring bloom (Fig. 7c). Total biomass of *Acartia* was characterized by the occurrence of two biomass peaks in a year; one in July, mainly formed from individuals of the second generation and another, small, in September, from individuals of the third generation. The numerical simulations show that the investigated species could not be the main factor limiting the phytoplankton spring bloom in the southern Baltic Sea, because the initial development was slow for *Acartia* and faster for *Pseudocalanus*, but main development formed after the bloom. However, the simulated microzooplankton biomass was enough high (i.e. maximum value ca. 30 mgC m^{-3} in May) to conclude, in our opinion, that, in this case, it was major cause limiting the spring bloom.

The results are significant changes in distributions of phytoplankton and zooplankton biomass which have taken place in an area of considerable increase of primary production. In the spring bloom time, a substantial growth of phytoplankton biomass is observed which slightly falls at the next stage as a result of an increase of zooplankton biomass mainly microzooplankton. The microzooplankton biomass reflects the phytoplankton availability, showing a strong increase with declining in food concentration. However, the later an increase of mesozooplankton biomass is caused by weight growth of successive cohorts and also the egg production by each of the female. This situation leads to the substantial growth in the total biomass of investigated species which is the algebraic sum of products of weights, W_i, and numbers, Z_i, ($Z_{\mathrm{meso}} = \sum_{k=1}^{2} \sum_{i=1}^{6} W_{k,i} Z_{k,i}$). These small maxima occurring in the distributions of *Pseudocalanus* and *Acartia* are the results mainly of a broad by successive cohorts causing their numbers Z_i to increase. Then, early juvenile of herring biomass growth tends to a decrease in micro- and mesozooplankton biomass. Any increase of predator biomass does not only depend on prey concentration but and an energy dissipation which in the upper mixed layer is defined by wind speed. At low prey levels, the rate of mortality is higher than growth and a decrease in predator biomass is observed.

8 Conclusions

The work presents the idea of 1-D-Coupled Ecosystem Model with a high-resolution zooplankton (herbivorous copepods) module for two taxa (*Pseudocalanus* and *Acartia*) as a top-down regulator may play a significant role in marine ecosystems, and the zooplankton community is diverse comprising large size differences and metabolic heterogeneity. It is therefore of importance to investigate and identify the critical factors. Such models are suitable as tools because hypothesis can be tested, and our understanding of processes and dynamics can be evaluated. The copepod model links trophic processes and population dynamics, and simulates individual growth within cohorts and the changes in biomass between cohorts.

Zooplankton have characteristic growth and development rates that are important in ecosystem dynamics and should be considered in ecosystem models. The model 1-D-NPZD presented by Dzierzbicka-Głowacka (2005a) describing temporal pattern for inorganic nitrogen concentration and phytoplankton biomass and *P. m. elongatus* in the spring bloom time in the Gdansk Gulf was a first step in this type of study.

In this paper, a population dynamics model for copepods was coupled with an one-dimensional physical and biological upper layer model to simulate the seasonal dynamics of *Pseudocalanus elongatus* and *Acartia spp.* in the Gdansk Deep, including in this model the equations not only for nutrients (total inorganic nitrogen and phosphate) and phytoplankton but for microzooplankton as one state variable and for small pelagic detritus and for an early juvenile of herring as predator, too. My model is a next step in understanding how the population dynamics of a dominant species interact with the environment.

The results of the numerical simulations of phytoplankton biomass and nutrient concentration described shortly here are in accordance with the in situ observations. The differences in the phytoplankton biomass between the modelled and mean observed values is equal to 5–20% in the 10 m upper layer and to 30% at the surface sea and depend on the month for which the calculations were made as well as depend on mainly

C/Chl ratio for converting the simulated carbon contents to chlorophyll-*a*. Comparing the nutrient concentration from the calculated and mean experimental data the present results indicate that the difference in Nutr is ca. 20% in the winter time, and ca. 5% in the summer time, in the upper layer; however, ca. 30% at the bottom.

However, the obtained depth integrated biomass of copepods is different in relation to mean value of observation data. The differences are in 20–30% range at the end of May after experimental data given by Mudrak (2004). In our opinion, on the basis of data from IMGW (see Maritime Branch Materials 2000), the total biomass of *Pseudocalanus* and *Acartia* computed here amount to ca. 50–60% of all copepods biomass in the Gdańsk Deep in 1999.

After all, the population dynamics model for *Pseudocalanus* and *Acartia* coupled with 1-D – Coupled Ecosystem Model can be utilized to study of the seasonal variability of above species in the southern Baltic Sea (Gulf of Gdańsk).

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References

Ambler, J. W.: Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana, from East Lagoon, Galveston, Texas, Estuar., cstl. Shelf Sci., 20, 743–760, 1985.

Bautista, B., Harris, R. P., Rodriguez, V., and Guerrero, F.: Temporal variability in copepod fecundity during two different spring bloom periods in coastal waters off Plymouth (SW England), J. Plankton Res., 16, 1367–1377, 1994.

Beckman, B. C. and Peterson, W. T.: Egg production of *Acartia tonsa* Dana in Long Island Sound, J. Plankton Res. 8, 917–925, 1986.

Berggreen, U., Hansen, B., and Kiørboe, T.: Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production, Mar. Biol., 99, 341–352, 1988.
Billen, G., Lancelot, C., and Maybeck, M.: N, P and Si retention along the aquatic continuum form land to ocean, in: Ocean Margin Processes in Global Change, edited by: Mantoura, R. F. C., Martin, J. M., and Wollast, R., Phys., Chem., Earth Sci. Res., Report 9, 19–44, Wiley and Sons, New York, 1991.
Carlotti, F. and Sciandra, A.: Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) couplong individual growth and larval development, Mar. Ecol. Prog. Ser., 56, 225–242, 1989.
Carlotti, F. and Nival, P.: Model of copepod growth and development: moulting and mortality in relation to physiological processes during an individual moult cycle, Mar. Ecol. Prog. Ser., 84, 219–233, 1992.
Carlotti, F. and Radach, G.: Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model, Limnol. Oceanogr., 41(3), 522–539, 1996.
Carlotti, F. and Wolf, K. U.: A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1-D ecosystem model, Fish. Oceanogr., 7(3/4), 191–204, 1998.
Ciszewski, P. and Witek, Z.: Production of older stages of copepods *Acartia bifilosa* Giesb. and *Pseudocalanus elongatus* Boeck in Gdańsk Bay, Pol. arch. Hydrobiol., 24, 449–459, 1977.
Checkley, D. M.: Food limitation of egg production by a marine planktonic copepod in the sea off southern California, Limnol. Oceanogr., 25, 991–998, 1980.
Christoffersen, K. and Jespersen, A. M.: Gut evacuation rates and ingestion rates of *Eudiaptomus graciloides* measured by means of the gut fluorescence method, J. Plankton Res., 8, 973–983, 1986.
Corkett, C. J. and McLaren, I. A.: The biology of *Pseudocalanus*, Ad. Mar. Biol., 15, 1–231, 1978.
Dagg, M. J. and Wyman, K. D.: Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus*, calculated from gut contents, Mar. Ecol. Prog. Ser., 13, 37–46, 1983.
Dam, H. G. and Peterson, W. T.: RThe effect of temperature on the gut clearance rate constant of planktonic copepods, J. Exp. Mar. Biol. Ecol., 123, 1–14, 1988.
Durbin, E. G., Durbin, A. G., Smayda, T. J., and Verity, P. G.: Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island, Limnol. Oceanogr., 28, 1199–1213,

1983.
Durbin, E. G. and Durbin, A. G.: Effects of temperature and food abundance on grazing and short-term weight change in the marine copepod *Acartia hudsonica*, Limnol. Oceanogr., 37, 361–378, 1992.
Dzierzbicka-Głowacka, L.: Numerical analysis of the influence of the grazing on the two-dimensional distribution function of the phytoplankton concentration in a stratified sea, Oceanologia, 36(2), 155–173, 1994.
Dzierzbicka-Głowacka, L.: Growth and development of copepodite stages of *Pseudocalanus spp.*, J. Plankton Res., 26, 49–60, 2004a.
Dzierzbicka-Głowacka, L.: The dependence of body weight in copepodite stages of *Pseudocalanus spp.* on variations of ambient temperature and food concentration, Oceanologia, 46, 45–63, 2004b.
Dzierzbicka-Głowacka, L.: A numerical investigation of phytoplankton and *Pseudocalanus elongatus* dynamics in the spring bloom time in the Gdansk Gulf, J. Mar. Syst., 53, 19–36, 2005a.
Dzierzbicka-Głowacka, L.: Modelling the seasonal dynamics of marine plankton in southern Baltic Sea. Part 1. A Coupled Ecosystem Model, Oceanologia, 47(4), 591–619, 2005b.
Dzierzbicka-Głowacka, L.: Equivalence of rates of growth and egg production of *Pseudocalanus*, Ocean. Hydrobiol. Stud., 34(4), 19–32, 2005c.
Dzierzbicka-Głowacka, L.: Encounter rate in zooplankton, Pol. J. Environ. Stud., 15(2), 243–257, 2006.
Fennel, W.: Modeling of copepods with links to circulation model, J. Plankton Res., 23, 1217–1232, 2001.
Fennel, W. and Neumann, T.: Variability of copepods as seen in a coupled physical biological model of the Baltic Sea, ICEM Marine Science Symposia, 219, 208–219, 2003.
Fey, D. P.: Differences in temperature conditions and somatic growth rate of larval and early juvenile spring-spawned herring from the Vistula Lagoon, Baltic Sea manifested in the otolith to fish size relationship, J. Fish. Biol., 58, 1257–1273, 2001.
Fennel, W.: Modeling of copepods with links to circulation model, J. Plankton Res., 23, 1217–1232, 2001.
Fennel, W. and Neumann, T.: Variability of copepods as seen in a coupled physical biological model of the Baltic Sea, ICES Marine Science Symposia, 219, 208–219, 2003.
Fransz, H., Moammerts, J. and Radach, G.: Ecological modelling of the North Sea, Nether J. Sea Res., 28, 67–140, 1991.

Frost, B. W.: A taxonomy of the marine calanoid copepod genus *Pseudocalanus*, Can. J. Zool., 67, 525–551, 1989.
Fryd, M., Haslund, O. H., and Wohlgemuth, O.: Development, growth and egg production of two copepod species *Centropages hamatus* and *Centropages typicus* in the laboratory, J. Plankton Res., 13, 683–689, 1991.
Hay, S. J.: Egg production and secondary production of common North Sea copepods: field estimates ith regional and seasonal comparisons, ICES J. Mar. Sci., 52, 315–327, 1995.
Hernroth, L.: Recommendations on methods for marine biological studies in the Baltic Sea. Mesozooplankton biomass assessment, The Baltic Marine Biologists, 10, 1–32, 1985.
Kiørboe, T., Møhlenberg, F., and Nicolajsen, H.: Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (lilljeborg) in relation to food concentration and temperature, Ophelia, 21, 181–194, 1982.
Kiørboe, T., Møhlenberg, F., and Hamburger, K.: Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action, Mar. Ecol. Prog. Ser., 26, 85–97, 1985.
Kiørboe, T. and Johansen, K.: Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. IV Zooplankton distribution and productivity in relation to hydrographic features,. Dana, 6, 37–51, 1986.
Klein Breteler, W. C. M., Gonzalesm S. R., and Schogt, N.: Development of Pseudocalanus elongatus (Copepoda, Calanoida) cultured at different temperature and food conditions, Mar. Ecol. Progr. Ser., 119, 99–110, 1995.
Kleppel, G. S., Holliday, D. V., and Pieper, R. E.: Trophic interactions between copepods and micoplankton: a question about the role of diatoms, Limnol. Oceanogr., 36, 172–178, 1991.
Kleppel, G. S.: Environmental regulation of feeding and egg production by *Acartia tonsa* off southern California, Mar. Biol., 112, 57–65, 1992.
Koski, M., Breteler, W. K., and Schogt, N.: Effect of food quality on rate growth and development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda, Calanoida), Mar. Ecol. Prog. Ser., 170, 169–187, 1998.
Kremer, J. N. and Nixon, S. W.: A coastal marine ecosystem. Simulation and analysis, Ecological studies 24, Springer-Verlag, Heidelberg, 1978.
Landry, M. R.: The development of marine calanoids with comment on the isochronal rule, Limnol. Oceanogr., 28, 614–624, 1983.
Last, J. M.: The food of four species of pleuronectiform larvae in the eastern English Channel

and southern North Sea, Mar. Biol., 45, 359–368, 1978a.
Last, J. M.: The food of three species of gadoid larvae in the eastern English Channel and southern North, Sea. Mar. Biol., 45, 377–386, 1978b.
Last, J. M.: The food of twenty species of fish larvae in the west-central North Sea. Fisheries Research Technical report, Lowestoft, 60, pp. 44, 1980.
Maritime Branch Materials Institute of Meteorology and Water Management, Environmental conditions in the Polish zone of the southern Baltic Sea during 1999, 2000.
Margoński, P.: The abundance, growth rate and mortality of the early life stages of herring (*Clupea harengus*) and smelt (*Osmerus eperlanus*) in the Vistula Lagoon (southern Baltic Sea) during 1998–1999, International Council for the Exploration of the Sea ICES CM 2000//N:21, 2000.
McLaren, I. A.: Generation lengths of some temperate marine copepods: estimation, production and implications, J. Fish. Res. Bd. Can., 345, 1330–1342, 1978.
McLaren, I. A., Corkett, C. J., and Zillioux, E. J.: Temperature adaptations of copepod eggs from the arctic to the tropics, Biol. Bull. 137, 486–493, 1969.
McLaren, I. A. and Leonard, A.: Assessing the equivalence of growth and egg production of copepods, ICES J. Mar. Sci., 52, 397–408, 1995.
McLaren, I. A., Sévigny, J. M., and Corkett, C. J.: Temperature-dependent development in *Pseudocalanus* species, Can. J. Zool., 67, 559–564, 1989.
Miller, T. J., Crowder, L. B., Rice, J. A., and Marshall, E. A.: Larval size and recruitment mechanisms in fishes: toward a conceptual framework, Can. J. Fish. Aquat. Sci., 45, 1657–1670, 1988.
Miller, C. A. and Landry, M. R.: Ingestion-independent rates of ammonium excretion by the copepod *Calanus pacificus*, Mar. Biol., 78, 263–270, 1984.
Moll, A. and Stegert, C.: Modelling *Pseudocalanus elongatus* stage-structured population dynamics embedded in a water column ecosystem model for the northern North Sea, J. Marine Syst., special issue AMEMR Symposium, in press, 2006.
Mudrak, S.: Short- and long-term variability of zooplankton in coastal Baltic water: using the Gulf of Gdańsk as an example, Ph. D. thesis, Gdańk Univ., Gdynia, (in Polish), 323pp., 2004.
Mudrak, S., Bielecka, L., and Żmijewska, M. I.: Diel vertical migrations of copepoda from Gdansk Deep (Baltic sea), Abstracts, 39th European Marine Biology Symposium, 2004 Genoa, 2004
Paffenhöfer, G. A.: Grazing and ingestion rates of nauplii, copepodids and adults of the marine

planktonic copepod *Calanus* helgolandicus, Mar. Biol. 11, 286–298, 1971.
Paffenhöfer, G.-A. and Harris, R. P.: Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck, J. Mar. Biol. Ass., UK, 56, 327–344,1976.
Peterson, W. T.: Rates of egg production by the copepod *Calanus marshallae* in the laboratoy and in the sea off Oregon, USA, Mar. Ecol. Prog. Ser., 47, 229–237, 1988.
Piontkovskii, S. A. and Petipa, T. S.: Quantitative description of the behavior of copepod *Acartia clausi* during feeding on algae, Soviet J. Mar. Biol., 2, 40–46, 1976.
Radach, G., Carlotti, F., and Spangenberg. A.: Variability of zooplankton population dynamics caused by annual weather variability, Fish. Oceanogr., 7(3/4), 272–281, 1998.
Renk, H.: Primary production in the southern Baltic, Sea Fisheries Institute, Gdynia, Poland, 2000.
Renk, H., Ochocki, S., and Pytel, H.: Short-term fluctuations of primary production and chlorophyll-a concentration in the Gdańsk Deep, Pol. Ecol. Stud., 9(3), 341–359, 1983.
Riley, G. A.: Factors controlling phytoplankton populations on Georges Bank, J. Mar. Res., 6, 54–73, 1946.
Riley, G. A.: A mathematical model of regional variations in plankton, Limnol. Oceanogr., 10, 202–215, 1965.
Roman, M. R.: Utilization of detritus by the copepod *Acartia tonsa*, Limnol. Oceanogr., 29, 949–959, 1984.
Rothschild, B. J.: Biodynamics of the sea: the ecology of high dimensionality systems, in: Toward a theory of biological – physical interactions in the world ocean, edited by: Rothschild, B. J., Kluwer, Boston, 527–548, 1988.
Runge, J. A.: Egg production of the marine planktonic copepod, *Calanus pacificus* Brodsky: laboratory observations, J. Exp. Mar. Biol. Ecol., 74, 53–66, 1984.
Runge, J. A.: Relationship of egg production of *Calanus pacificus* to seasonal changes in phytoplankton availability in Puget Sound, Washington, Limnol. Oceanogr., 30, 382–396, 1985.
Sciandra, A.: Study and modelling of development of *Euterpina acutifrons* (Copepoda, Harpacticoida), J. Plankton Res., 8, 1149–1162, 1986.
Schmidt, K., Kähler, P., and Bodungen, B.: Copepod egg production rates in the Pomeranian Bay (southern Baltic Sea) as a function of phytoplankton abundance and taxonomic composition, Mar. Ecol. Prog. Ser., 174, 183–195, 1998.
Sekiguchi, H., McLaren, I. A., and Corkett, C. J.: Relationship between growth rate and egg

production in the copepod *Acartia clausi* Hudsonica, Mar. Biol., 58, 133–138, 1980.
Steele, J. H.: The Structure of Marine Ecosystems, Harvard University Press, Cambridge, 1974.
Steele, J. and Henderson, E. W.: Simulation of vertical structure in a planktonic ecosystem, Scott. Fish. Res. Rep., 5, 1–27, 1976.
Steele, J. H. and Mullin, M. M.: Zooplankton dynamics, in: The sea Vol 6, edited by: Goldberg, E. D., McCave, I. N., O'Brien, J. J., and Steele, J. H., Interscience Publ. New York, London, Sydney, Toronto, 857–887, 1977.
Stoecker, D. K. and Egloff, D.A.: Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers, J. Exp. Mar. Biol. Ecol., 110, 53–68, 1987.
Thompson, B. M.: The biology of *Pseudocalanus elongatus* (Boeck). Ph.D. Thesis, University of East Anglia, Norwich, 1976.
Thompson, B. M.: Growth and development of *Pseudocalanus elongatus* and *Calanus* sp. in the laboratory. J. Mar. Biol. Ass., UK, 62, 359–372, 1982.
Thompson, A. M., Durbin, E. G., and Durbin, A.G.: Seasonal changes in maximum ingestion rate of *Acartia tonsa* in Narragansett Bay, Rhode Island, USA, Mar. Ecol. Prog. Ser., 108, 91–105, 1994.
Turner, J. T. and Tester, P. A.: Zooplankton feeding ecology: nonselective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pileatus* giesbrecht in the plume of the Mississippi River, J. Exp. Mar. Biol. Ecol., 126, 21–43, 1989.
Witek, Z.: Structure and function of marine ecosystem in the Gda/nsk Basin on the basis of studies performed in 1987, Scientific Committee on Oceanic Research, 63, 1–123, 1993.
Witek, Z.: Biological production and its utilization within a marine ecosystem in the western Gdansk basin, Sea Fischeries Institute, Gdynia, Poland, 1995.
Wlodarczyk, E., Durbin, A. G., and Durbin, E. G.: Effect of temperature on lower feeding thresholds, gut evacuation rate, and diel feeding behavior in the copepod *Acartia hudsonica*, Mar. Ecol. Prog. Ser., 85, 93–106, 1992.
Wroblewski, J. S.: Formulation of growth and mortality of larvae of northern anchovy in a turbulent feeding environment, Mar. Ecol. Prog. Ser., 20, 13–22, 1984.
Wroblewski, J. S. and Richman, J. G.: The non-linear response of plankton to wind mixing events – implications for survival of larval northern anchovy, J. Plankton Res., 9, 103–123, 1987.
Verity, P. G. and Smayda, T. J.: Nutritional value of *Phaeocystis pouchetii* (Prymnesiophyceae)

and other phytoplankton for *Acartia* spp. (Copepoda): ingestion, egg production, and growth of nauplii, Mar. Biol., 100, 161–171, 1989.

Vidal, J.: Physioecology of Zooplancton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp., Mar. Biol., 56, 111–134, 1980a.

Vidal, J.: Physioecology of Zooplancton. II. Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp., Mar. Biol., 56, 135–146, 1980b.

Vinogradov, M. E. and Shushkina, E. A.: Functioning of pelagic plankton communities in the ocean. Nauka Moskwa (in Russian), 1987.

Załachowski, W., Szypuła, J., Krzykawski, S., and Krzykawska, I.: Feeding of some commercial fishes in the southern region of the Baltic Sea in 1971 and 1972, Pol. Arch. Hydrobiol., 22, 429–448, 1975.

Table 1. Differential equations for pelagic detritus and new processes; PDetr(z, t): detritus concentration, K_z: turbulent diffusion coefficient, w_z: phytoplankton sinking velocity, w_d: detritus sinking velocity, r_d: detritus remineralization rate.

$$\frac{\partial \mathrm{PDetr}}{\partial t} = \frac{\partial}{\partial z}\left(K_z \frac{\partial \mathrm{PDetr}}{\partial t}\right) + \mathrm{MOR}_{PD} + \mathrm{FEC}_{TD} + \mathrm{MOR}_{TD} - w_d \frac{\partial \mathrm{PDetr}}{\partial z} - \mathrm{ING}_D - \mathrm{REMI}_D$$

Food available for mezozooplankton	$\mathrm{Foot}(z,t) = Phyt(z,t) + \mathrm{PDetr}(z,t)$
Inputs to the pelagic detritus equation with microzooplankton equation:	
Fecal pellet material	$\mathrm{FEC}_Z = n_f \mathrm{ING}_Z$
Carcasses material	$\mathrm{MOR}_Z = n_z \mathrm{ING}_Z$
with mesozooplankton equation given in Table 3	
Pelagic detritus equation	
Sinking of pelagic detritus	$w_d \frac{\partial \mathrm{PDetr}}{\partial z}$
Flux of dead phytoplankton	$\mathrm{MOR}_{PD} = p_p \mathrm{MOR}_P$
Flux of fecal pellets	$\mathrm{FEC}_{TD} = p_f(\mathrm{FEC} + \mathrm{FEC}_Z)$
Flux of dead zooplankton and fish	$\mathrm{MOR}_{TD} = p_z(\mathrm{MOR} + \mathrm{MOR}_Z)$
Copepod grazing on pelagic detritus	$\mathrm{ING}_D = \mathrm{ING} \frac{\partial \mathrm{PDetr}(z,t)}{\partial \mathrm{Foot}(t)}$
Remineralization of pelagic detritus	$\mathrm{REMI}_D = r_d \mathrm{PDetr}$
Nutrient equation	
Total remineralization	$\mathrm{REMI} = \mathrm{REMI}_D$
Benthic detritus equation	
Flux condition at the boundary for phytoplankton and detritus	$F_P(H) = -w_z Phyt(H,t) - w_d \mathrm{PDetr}(H,t)$

Table 2. Mathematical formulations of relationships used in the model; i: cohort; j: stage; if $W_{j-1}<W_i<W_j$ then $i=j$ for successive developmental stages $j=1, 2 \cdots 13$; Foot: food concentration; T: temperature; W_i: weight; Z_i: number; B: predator biomass; g: growth rate of predator; W_{female}: weight of female; W_{egg}: weight of egg; K_z: turbulent diffusion coefficient; Ri: Richardson number.

Process	Units	Formulation
Growth		
Ingestion	μgC d^{-1}	$\mathrm{ING}_i = fil_i fte_i fw_i$
Influence of food		$fil_i(\mathrm{Foot}) = \mathrm{f}_{\mathrm{i}_{max}}\{1-\exp\left(\frac{-(\mathrm{Foot}-\mathrm{Foot}_o)}{\mathrm{k}_{\mathrm{Foot}}}\right)\}$
Influence of temperature		$fte_i(T)=t_1 t_2^T$
Allometric relation		$fw_i(W)=W_i^{\alpha}$
Fecal pellets	μgC d^{-1}	$\mathrm{FEC}_i=(1-n_a)\mathrm{ING}_i=n_f\mathrm{ING}_i$
Metabolism	μgC d^{-1}	$\mathrm{MET}_i=M_s+M_a$
Basic metabolism		$M_s=n_w W_i$
Active metabolism		$M_a=n_e A_i$, $A_i=n_a\mathrm{ING}_i$
Egg matter	μgC d^{-1} female^{-1}	$\mathrm{ProdEgg}_i=\exp(\mathrm{GROWTH})-1$
Growth	μgC d^{-1}	GROWTH=ING-FEC-MET
Growth $j=13$	μgC d^{-1}	$\mathrm{GROWTH}_{13}=\mathrm{ING}_{13}$-$\mathrm{FEC}_{13}$-$\mathrm{MET}_{13}$-ProEgg
Dynamics		
Mortality	no. m^{-3} d^{-1}	$\mathrm{MOR}_i=Z_i m_z$
Predation	no. m^{-3} d^{-1}	$\mathrm{PRED}_i=\beta g B/W_i$
Migration	no. m^{-3} d^{-1}	$\mathrm{MIG}_i=1+a_w\cos(\omega(t-t_o))f(z)$
Eggs	no. d^{-1} female^{-1}	$\mathrm{EGG}_i=\frac{W_{\mathrm{female}}}{W_{\mathrm{egg}}}\mathrm{ProdEgg}_i$, $\mathrm{EGG}=X\,Z_{13}\int_J \mathrm{EGG}_i$
Turbulent diffusion	m^2 s^{-1}	$K_z=5\times10^{-4}(1+Ri)^{-2.5}+10^{-6}$

Table 3. Processes coupling the mesozooplankton submodel to the other components.

Total ingested material	$\mathrm{ING}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{ING}_{k,i}Z_{k,i}$
Total fecal pellet material	$\mathrm{FEC}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{FEC}_{k,i}Z_{k,i}$
Total cadaverous material	$\mathrm{MOR}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{MOR}_{k,i}W_{k,i}$
Total metabolic products	$\mathrm{MET}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{MET}_{k,i}Z_{k,i}$

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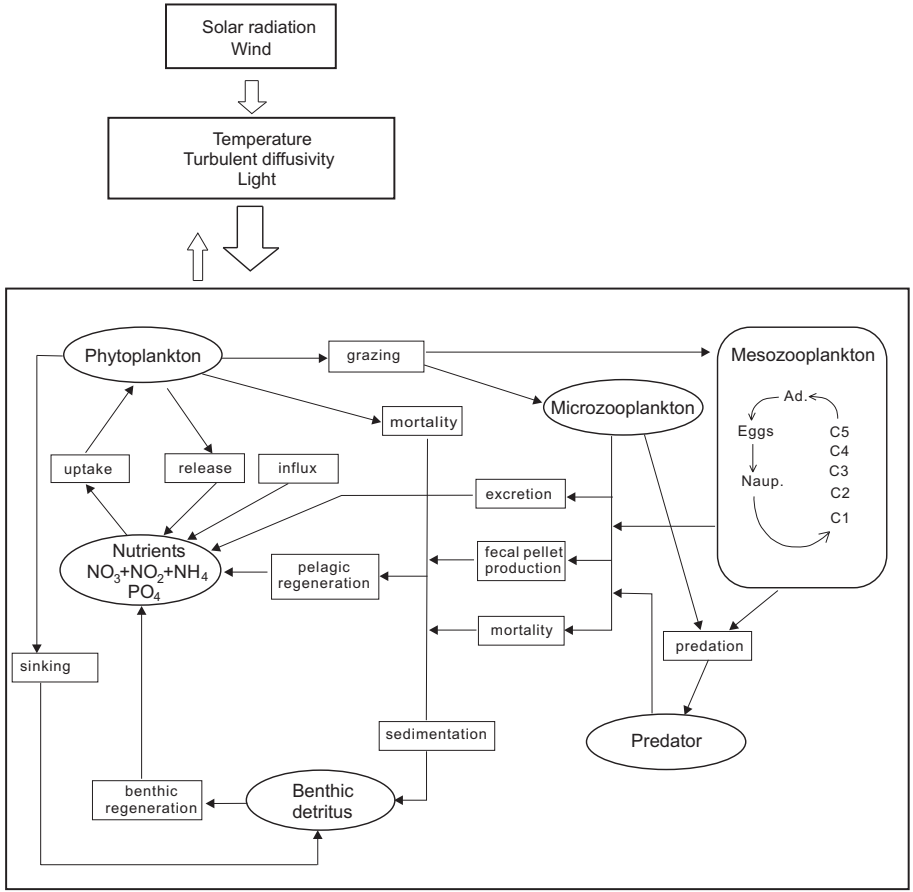

Fig. 1. Conceptual diagram of the coupled model.

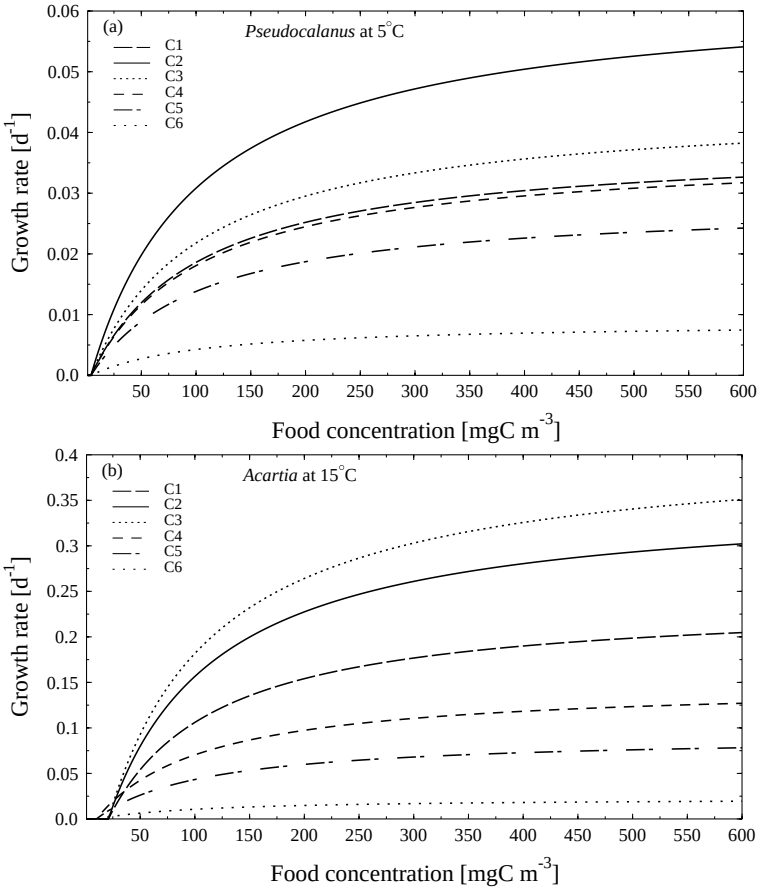

Fig. 2. Growth rate as a function of food concentration at 5°C for *Pseudocalanus minutus elongatus* **(a)** and at 15°C for *Acartia spp.* **(b)**.

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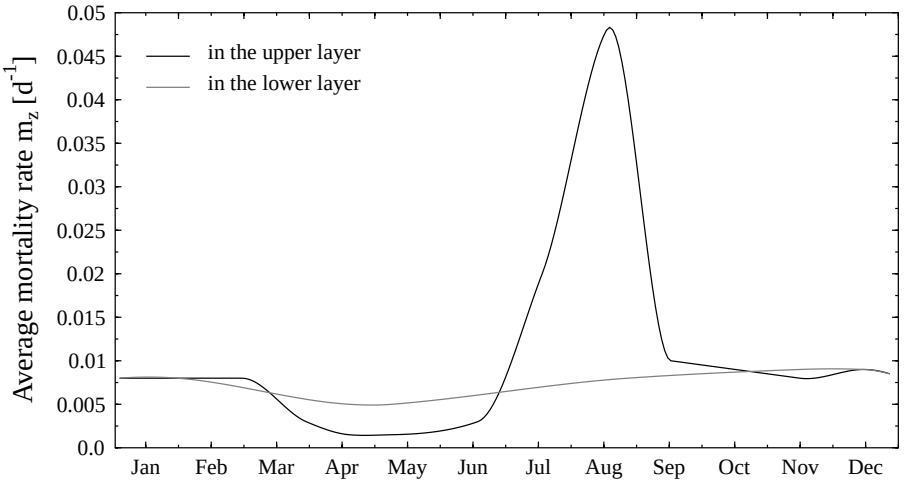

Fig. 3. Mortality rate of *Pseudocalanus* in the upper and lower layer.

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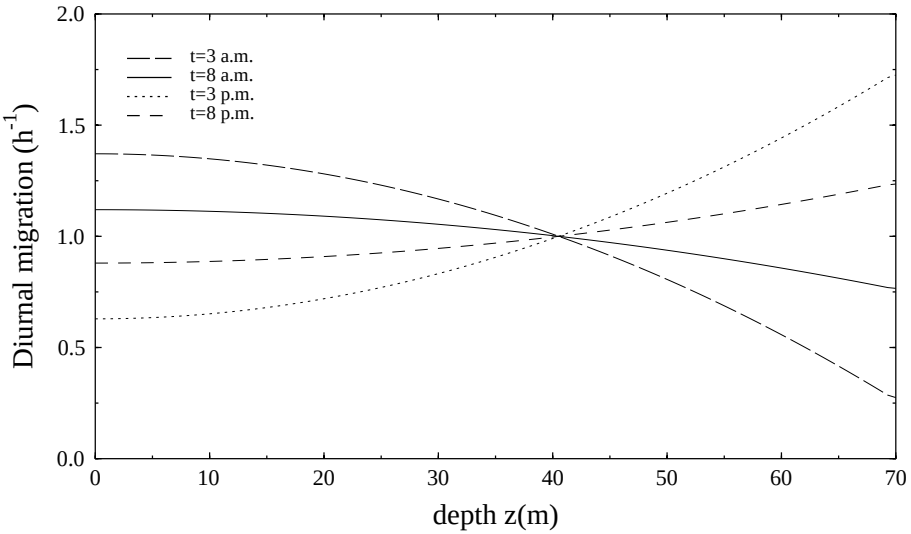

Fig. 4. Daily migration rate as a function of depth at 03:00 a.m., 09:00 a.m., 03:00 p.m. and 09:00 p.m.

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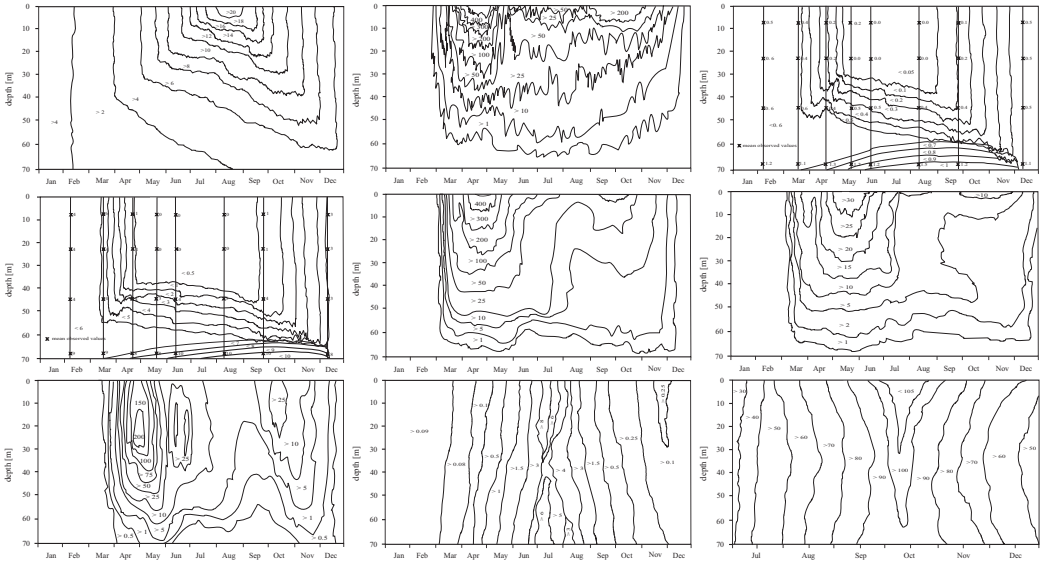

Fig. 5. Annual simulation. Simulated profiles of temperature **(a)**, primary production **(b)**, nutrients – total inorganic nitrogen **(c)** and phosphate **(d)**, phytoplankton (e), microzooplankton **(f)**, small detritus **(g)**, mesozooplankton – *Pseudocalanus elongatus* and *Acartia spp.* **(h)** and early juvenile of herring **(i)** at the Gdansk Deep in 1999.

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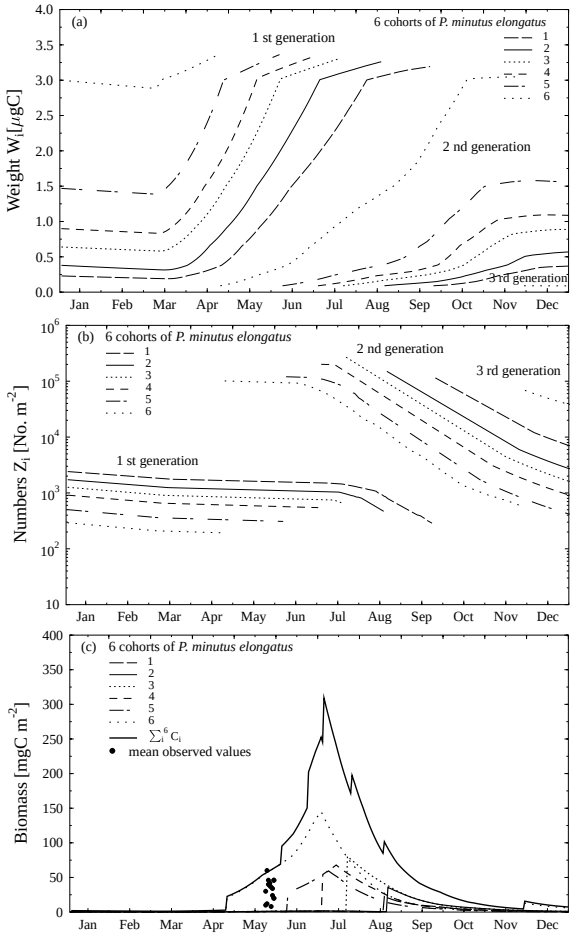

Fig. 6. *Pseudocalanus minutus elongatus*. Weights, W_i **(a)**, numbers, Z_i **(b)**, and biomass, $\sum W_i Z_i$ **(c)**, of six cohorts.

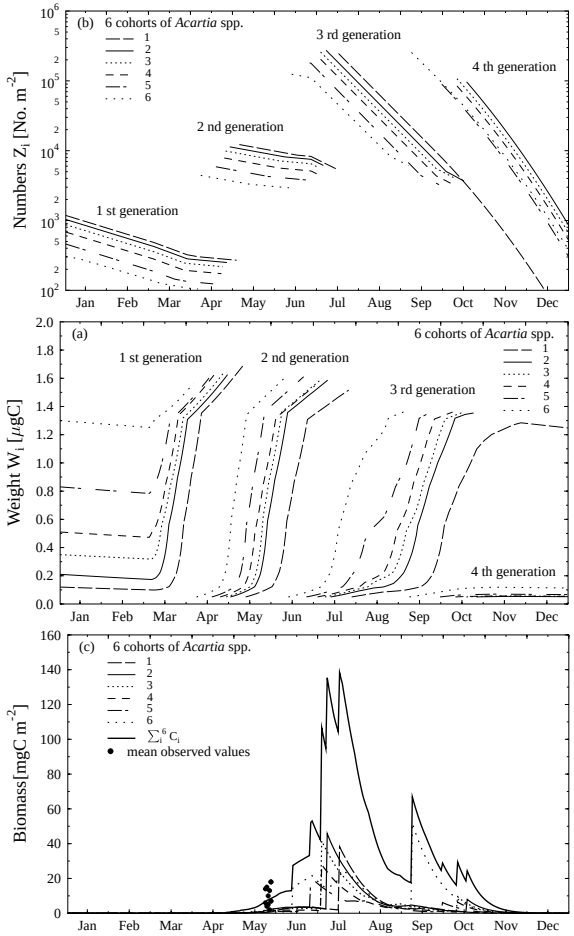

Fig. 7. *Acartia spp.* Weights, W_i **(a)**, numbers, Z_i **(b)**, and biomass, $\sum W_i Z_i$ **(c)**, of six cohorts.

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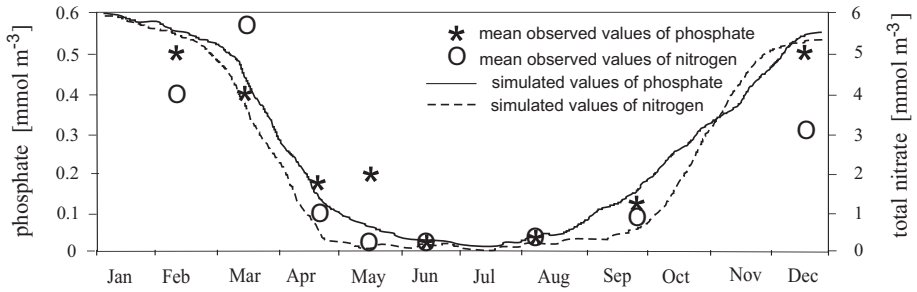

Fig. 8. Simulated and mean observed values of nutrient in the 15 m upper layer at the Gdańsk Deep in 1999.

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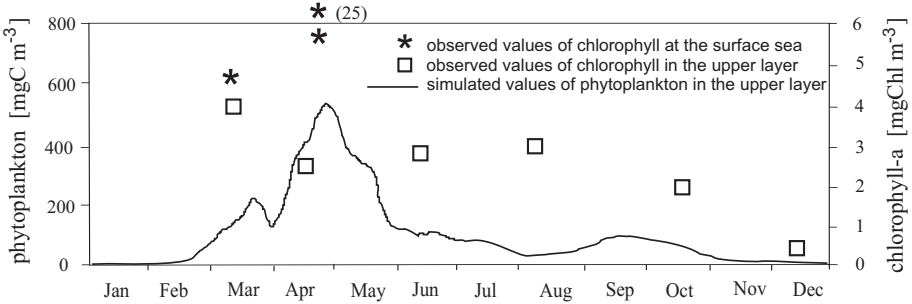

Fig. 9. Simulated values of phytoplankton biomass and mean observed values of chlorophyll-*a* in the upper layer at the Gdańsk Deep in 1999.

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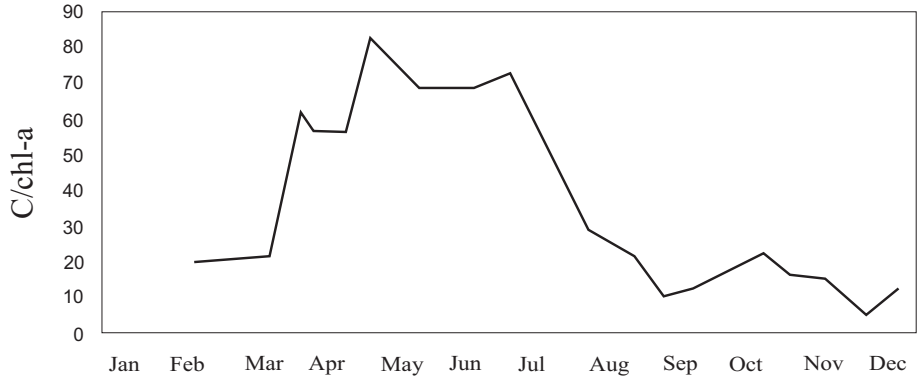

Fig. 10. Carbon-to-chlorophyll-*a* ratio in phytoplankton at atation in the Gdańsk Gulf in the 0–15 m layer (Witek, 1993).